SCIENCE

FRIDAY, JANUARY 28, 1916

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THE ISTHMUS OF PANAMA IN ITS RELATION TO THE ANIMAL LIFE OF NORTH AND SOUTH AMERICA[1]

IT is a commonplace of geological teaching that the past can be understood only through a knowledge of the present and it is equally true that the present can be fully comprehended only through a knowledge of the past. Each must be employed to elucidate the other and we must pass from one to the other, as new discoveries are made in either realm.

The problems which deal with the existing geographical distribution of animals have received much light from the progress of paleontological discovery and the present arrangement is clearly seen to be the necessary outcome of an illimitable series of past changes, climatic, geographical and biological. Even in pre-Darwinian days the geographical distribution of animals had been given much attention, as a collection of interesting facts, though, under the belief in special creation then prevailing, no explanation of those facts was possible. The general adoption of Darwin's views immediately placed the subject in a new light, for it was at once seen that, unless the theory of evolution could offer a rational and satisfactory solution of these problems of distribution, the foundations of the theory would be greatly weakened.

No result of paleontological studies has, of late years, been more striking than the clear recognition of the fact that migra-

[1] Lecture before the American Association for the Advancement of Science at its San Francisco meeting, August, 1915.

tions from continent to continent have played a highly significant part in bringing about the present geographical arrangement of animals and plants. This conception was first suggested by Cuvier, who, however, would seem not to have attached great importance to it, and it fell into neglect together with his theory of Catastrophism. Present geographical distribution is, when well understood, in itself a partial record of those past changes, partial, because of the extinction of many forms which, in every region, once existed, but have completely vanished. Such migrations from continent to continent were, it should be distinctly understood, radically different in character from the annual migrations of birds, and it is unfortunate that the same term should be used to designate such very distinct classes of facts. The so-called migrations with which we have to deal, such as those of mammals, are a purely unconscious and unintentional spread into new areas, as the increasing number of individuals of a given species begin to press upon the sources of food-supply. This spread will continue from generation to generation until insuperable barriers are encountered and there the spread must cease, unless some geographical or climatic change should remove the barrier, when the spread will continue. For nearly all land animals the most impassable of barriers is the sea, even in narrow arms, though the climatic factors of temperature and, in somewhat less degree, moisture are of almost equal importance. In the long course of geological time and even in its later portion, with which we are here more particularly concerned, both the relations of the various continents to one another and climatic conditions have undergone great and repeated changes, and it is those changes, with their consequently varying possibilities of intermigration, which are registered in the geographically composite fauna of almost every great land area of the earth. Enough has been already learned regarding the history and development of the various mammalian groups to make it plain that the mammals of each different continent form a sort of mosaic, the parts of which are of the most diverse places of origin and dates of immigration. The geological date largely determines the amount and kind of modification which the creatures have undergone in their new homes.

In attempting to estimate the significance of these facts, one assumption must be made, an assumption for which there is a large and increasing body of evidence, namely, that, in the higher animals at least, the same group never originated independently, from ancestors either similar or different, in two disconnected regions. It is perfectly true that parallel and convergent modes of development have always been important factors in the evolutionary process, and no one is more firmly persuaded of this than the paleontologist, but there is no reason to believe that these modes of development ever went so far as to produce substantially identical results in separate land areas. These principles are best illustrated by the mammals, simply because the past geological history of that group has been ascertained more fully and continuously than that of any other class of animals.

The scheme for dividing the land surface of the globe into zoological regions, in accordance with the distribution of animals and especially of mammals, has been the subject of much controversy, but now a general agreement has been reached. Thus, the very long isolation of Australia is recognized by setting off that continent and its adjoining islands, in contradistinc-

tion to all the rest of the world; it is the empire of marsupials and monotremes, while the other continents together constitute the empire of the placental mammals. This placental empire is, in turn, very unequally divided into two realms; the first, called *Arctogœa,* comprises North America, Europe, Asia and Africa and has an unmistakable general similarity in its mammals, in contrast to the second realm, *Notogœa,* which includes South and Central America and the West Indies. After Australia, Notogæa is zoologically the most peculiar region of the earth, a peculiarity which is likewise due to its long separation from the continents of Arctogæa.

The frequently made and interrupted communication of North America with the eastern hemisphere, principally by way of a land which occupied the site of the present shallow Bering Sea, is reflected in the geographically composite character of its mammalian fauna. This connection allowed intermigrations of animals between the eastern and the western hemispheres, each furnishing to the other elements which still persist in their new homes, though often becoming extinct in their places of origin. For example, the horses and camels have disappeared from North America, although they passed through the greater part of their development in that continent. The last of these migrations, which took place in the Pleistocene epoch, brought in such a host of Old World types, that the northern half of North America, comprising the Arctic and Boreal Zones of Merriam, belongs zoologically to the great Holarctic Region, which includes Europe, northern Africa and all of Asia except its southern peninsulas and thus encircles the earth.

The characteristic part of North America is the Sonoran Region, roughly the United States and the Mexican plateau, and ever this region contains many Old World forms, immigrants which arrived here at very different geological dates and, in accordance with the length of their stay here, have become more or less extensively modified. With these are associated many indigenous types, derived from a long North American ancestry and a very few migrants from South America, the short-tailed porcupine, probably the opossums, and in southeastern Texas an armadillo. These southern animals are the insignificant remnant of a great immigration which entered North America from the south, but was not able to gain a lasting foothold here.

South American mammals are obviously divisible into two radically different assemblages, one of which is related to the types characteristic of Arctogæa and the other is entirely peculiar to Notogæa. The first, or immigrant, assemblage comprises all the beasts of prey, the wolves, cats, otters, skunks and one species of bear; all of the hoofed animals, the tapirs, peccaries, deer, and that remarkable section of the camel family, the guanacos, llamas, etc.; among the rodents, the rabbits, squirrels, rats and mice. The second, or indigenous, series includes the opossums, the highly characteristic edentates, sloths, armadillos and anteaters, and a very large number of peculiar rodents, all of which belong to the porcupine group, tree-porcupines, chinchillas, cavies, water-hogs, etc., etc. The paleontological history of South American mammals amply justifies the distinction of these two assemblages as immigrant and autochthonous and shows that South America derived from the north a much larger proportion of its modern mammals than North America did from the south.

It is altogether probable that in the Mesozoic Era all of the continents were

directly or indirectly connected with one another, though it is not necessary to suppose that these connections all existed at the same time. In the Cretaceous Period every continent, even Australia, had its Dinosaurs, huge, slow-moving, land reptiles, which could not have crossed wide arms of the sea, but were dependent for their spread upon continuity of land. It may likewise be assumed that the minute and primitive mammals of the Mesozoic had a similar, world-wide distribution, though the data are still too scanty to permit any positive statements with regard to them. Early in the Tertiary Period of the Cenozoic Era, South America was completely cut off from any land communication with North America, assuming that such communication had previously existed, as it probably had. Thenceforward and for a very long period of time, the faunas of the two American continents developed in entire independence of each other and with remarkably different results.

To the student who is familiar with the Oligocene and Miocene mammals of the northern hemisphere, it is like entering a new world, when he begins to examine the mammalian faunas of the Deseado and Santa Cruz formations of Patagonia. In any comparison between the homotaxial faunas of North America and Europe, the differences are in species and genera, less commonly of families, but between South America and the northern hemisphere it is mainly a difference of orders. These Patagonian faunas contain no Carnivora, Artiodactyla, Perissodactyla or Proboscidea, the groups which were most abundant in Arctogæa. Beasts of prey were numerous and varied, but they were all predaceous marsupials; two other groups of marsupials, the opossums and cœnolestids, were also common, at a time when the whole order had vanished from the northern hemisphere, apparently even from North America. An extremely abundant, diversified and conspicuous element of the fauna, especially in the Santa Cruz and subsequent formations, was the characteristic South American order of the Edentata, which included the ground sloths, armadillos and glyptodonts, none of which appeared in the northern hemisphere till a long subsequent period, with the doubtful exception of the armadillos. True sloths and anteaters have also been reported by Ameghino from the Santa Cruz, and although the evidence for this determination is insufficient, it is altogether probable that these groups were already in existence in the forested regions of the north, if not on the plains of Patagonia, which would seem to have had but few trees at that time. At all events, arboreal animals are rare or absent from the fauna.

The very large assemblage of hoofed animals all belonged to groups which are now altogether extinct and no member of which has ever been found outside of South and Central America, the toxodonts, typotheres, homalodotheres, astrapotheres and litopterns, a wonderful series, which took the place of the hoofed mammals of Arctogæa and would appear to have been strictly autochthonous. Aside from the Insectivora, which, as being of great geological antiquity and nearly cosmopolitan in their distribution, have little bearing on the problems with which we are now concerned, only two mammalian orders occurred in the Santa Cruz fauna which at the same time existed in the northern hemisphere, the rodents and the monkeys. The remarkably diversified and numerous rodents all belonged to the Hystricomorpha, or porcupine-group, of which North America never had a representative until the coming in of the great immigration from the south and to-day has only the short-tailed porcupine. South

America then had no hares, rabbits, pikas, squirrels, marmots, beavers, rats or mice, but in place of them had a host of cavies, chinchillas, agoutis, and several other families, all of which still abound in the southern continent. The South American monkeys present a problem of much difficulty; all our present knowledge justifies us in saying that they could not have come from North America, for that continent never had any monkeys and even the lemurs became extinct here after the Eocene.

The Miocene faunas of North America are in the sharpest possible contrast to those of South America. They contained several families of true Carnivora, wolves of many diverse kinds, saber-toothed tigers and true cats, weasels, martens, otters, raccoons, and the like; a great abundance and variety of hoofed animals belonging to the artiodactyls and perissodactyls, horses, tapirs, rhinoceroses, chalicotheres, peccaries, camels, llamas, deer, antelopes and certain families, such as the highly characteristic oreodonts, which are now extinct, while the earliest of American mastodons had already made their way in from the Old World. The rodents, though including some very bizarre forms, now extinct, all belonged to the familiar northern families, rabbits, squirrels, marmots, beavers, pocket-gophers, jumping mice, kangaroo rats, vesper mice, etc., etc. There were no marsupials, edentates (with an exception to be noted subsequently), monkeys, rodents of the southern families, nor any of the remarkable hoofed animals which then swarmed in such multitudes in South America. Nothing could be more obvious or more assured than the conclusion that the two Americas had long been so completely separated that no migration of land animals from one to the other was possible and, in this long interval, the operation of divergent evolution had brought about this total disparity and unlikeness of faunas.

The junction of the two Americas, by way of the Isthmus of Panama, would seem to have been effected early in the Miocene epoch, or possibly even at the close of the Oligocene, and then began the slow process of the intermigration of land animals in both directions. The earliest indication of the animal of Notogæan forms in North America is the claw of a ground-sloth, discovered by Sinclair in the middle Miocene of Oregon but it was not till the Pliocene and, more strikingly, in the Pleistocene, that the southern immigrants arrived in large numbers, and in South America no northern types have been found in beds older than the Paraná formation, which I believe to be Pliocene, but which may prove to belong to the later Miocene.

As thus recorded, the process of mammalian diffusion might seem to be incredibly slow, but there are several considerations which help to explain the extreme tardiness with which the exchange of animals between the two continents was carried on. (1) The Miocene mammalian faunas which have as yet been recovered are in the far north and the far south and we know nothing of the intermediate regions, Central America, northern and middle South America. (2) As previously pointed out, the so-called migration of mammals is merely a gradual spread, a wider and wider range, as increasing numbers demand fresh sources of food. (3) For a considerable period after the upheaval of a sea-bottom into land, it must remain impassable to most mammals, because devoid of vegetation, and until plants have taken possession of it, it can serve as only an imperfect and difficult means of communication. (4) Another and very important obstacle to migration between the Americas was that it took place along the lines of longitude

and thus encountered differences of climate, which are among the most effective barriers to the spread of mammals, while between North America and the Old World the migrations followed the lines of latitude and therefore, to all appearances, were accomplished much more quickly. (5) Finally, it is not to be supposed that the fossils already discovered make up anything like a complete list. Doubtless, many things still remain to be found, and others, because of rarity or some other unfavorable circumstance, failed altogether of preservation, and the actual progress of diffusion may well have been more rapid and effective than the observed facts would lead us to suppose.

In the middle and later Pliocene and still more in the Pleistocene the intermigration had proceeded so far that the two continents possessed a very considerable number of mammalian genera in common, as immediately appears from a comparison of the faunal lists. The movement culminated in the Pleistocene, where the number of southern forms in the northern continent and of northern forms in the southern lands reached its maximum. In both continents the Pleistocene mammalian fauna was a very much richer and more varied assemblage than the modern one, for the great and mysterious extinctions which came late in the epoch and at its close, devastating more than three fifths of the land surface of the earth, were especially severe in North America and left that continent in a zoologically impoverished state. Beside almost all of the existing mammals which still continue to inhabit the region, Pleistocene North America had mastodons, three species of elephants, several tapirs and ten species of horses, ranging in size from small ponies to species which exceeded the largest modern draught horses. Peccaries spread as far north as Pennsylvania and from ocean to ocean and were accompanied by great herds of camels and llamas. Seven species of bison, some of them far surpassing the existing buffalo, so-called, were distributed from Florida to Alaska, while musk-oxen and allied forms extended far to the south and along the Pacific coast into California. Modern types of deer and antelopes were associated with several extinct types, some of which must have been very grotesque in appearance. Especially remarkable is the discovery by Gidley in western Maryland of an antelope which is hardly distinguishable from the recent African Eland. Almost all the existing North American beasts of prey have been found in the Pleistocene, but there were many more that are now extinct and were of extraordinary size and power; giant wolves, lions, the terrible saber-toothed tigers and the huge short-faced bears are examples of these vanished forms, the disappearance of which made life much easier for early American Man.

All of the animals so far enumerated are typically Arctogæan in character and were either immigrants from the Old World, of various geological dates of arrival, or were of indigenous North American ancestry and development, but mingled with those were many South American mammals, the history and evolution of which can be followed in satisfactory detail in the successive Tertiary formations of that continent. The strangest and most conspicuous of those migrants from the south were the great edentates. The huge, elephantine ground-sloths, a group now entirely extinct, but very abundant in the Pleistocene of both North and South America, ranged all across the continent from Pennsylvania to California. The genus *Megalonyx,* which, it is interesting to note, was first named by Thomas Jefferson from some bones found in Virginia, would seem to

have been a forest-living creature, and, so far as is now known, was confined to the region east of the Mississippi River. The almost equally massive *Mylodon* replaced it over the Great Plains and on the Pacific coast, particularly fine specimens occurring in the wonderful asphalts of Rancho la Brea, which the work of Professor J. C. Merriam has rendered so celebrated. A third genus, *Megatherium,* of even greater size and heavier proportions, extended into Georgia and South Carolina, but is not known farther north, as it was probably unable to endure a cold climate. Those most grotesque beasts, the Glyptodonts, which were like enormous armadillos in appearance, accompanied the ground-sloths in their migration to North America, but have been found only in the southern states, from Florida to Texas and Mexico, being doubtless limited in their northward range by the barrier of climate.

The Pleistocene rodents tell a similar story. Practically all of the modern forms were already here and associated with these were certain strange and curious forms, like the giant beaver, of northern origin, but now extinct, and a few South American immigrants, like the short-tailed porcupines and the water-hogs, of which only the former have survived. The marsupial group of the opossums had in the Eocene epoch extended over Europe and the Americas, but none have been found in North America in beds later than the Oligocene. Of course such small animals may have merely escaped the collector's eye, but, taking all things into consideration, it is probable that the group vanished completely from the northern hemisphere and returned with the immigration from South America, where they had continued to flourish without interruption.

The Pleistocene fauna of South America was likewise much richer and more varied, especially in very large mammals, than is the existing one, and is far stranger than the corresponding one of North America, differing more radically from that of modern times, for the extinctions swept away not only species and genera, but whole families and orders as well. The pampas of Argentina, the caverns of Brazil and, in lesser degree, areas in Bolivia and Ecuador, have yielded a marvelous series of Pleistocene mammals, which give a very striking picture of the life of the times. The same distinction between immigrant and autochthonous types which was noted in the existing fauna of South America was as strongly marked in the Pleistocene. Beside those northern immigrants which have maintained their foothold in the southern continent and are represented there to-day, there are many others which are now extinct, some of those groups which have become altogether extinct, others which have vanished from the western hemisphere, or from South America only. The Pleistocene fauna had substantially all of the mammals which still inhabit Notogæa and it is therefore unnecessary to repeat the names of those which form part of the modern fauna. It may be noted, however, that some of the recent families had representatives much larger in size than any that now exist, such as the monkeys and the raccoons, above all, the armadillos.

Some of these extinct immigrants were very abundant and conspicuous in the Pleistocene. The great saber-toothed tigers ranged all the way from Pennsylvania and California to the Argentinian pampas and were accompanied by the short-faced bears. A strange feature was the presence of a wolf which is apparently referable to the same genus (*Cyon*) as the wild dog or Dhole, of recent India. Horses were very common wherever Pleistocene fossils have

been found and must have arrived in South America at a relatively early date, for several highly peculiar and aberrant types were developed. One of these (*Hyperhippidium*) found in the Andes, was a small, mountain horse, with remarkably short feet which were well adapted to climbing. Tapirs ranged down into Argentina, much farther south than at present, but were not otherwise noteworthy. The range of the llamas also was much greater than it is to-day; now, they are restricted to the colder parts of the continent, but in the Pleistocene they extended into the forests of Brazil. Two antelopes have been reported, a family of which Notogæa has now no representatives. Mastodons of several species have been found in many parts of the continent, but, curiously enough, the true elephants did not accompany them in their southward migration. Why this was, it is difficult to say; perhaps because the North American elephants, which came in by way of Siberia, were cold-country species and therefore unable to cross the tropics.

The Pleistocene extinctions worked even greater havoc among the autochthonous forms than among the immigrants, destroying almost all of the very large mammals whose history and development may be traced back, step by step, through the successive divisions of the South American Tertiary. The visitor to the museums of La Plata and Buenos Aires can not but be deeply impressed by the number and variety of the ground-sloths and glyptodonts from the Pampean formation which are there displayed; it is immediately evident that the members of those groups which inhabited Pleistocene North America were but the outlying stragglers of the far more numerous and incomparably more diversified assemblage found in South America. They were indeed a strange and grotesque host of ponderous, slow-moving, but inoffensive plant-feeders, which, together with the almost equally bizarre indigenous hoofed animals, gave a most outlandish character to the fauna. The ground-sloths ranged in size from a tapir to a short-legged elephant; *Megatherium* even surpassing the elephants in massiveness of trunk and limbs. The glyptodonts differed much among themselves in size, in the character of the head, in the form of the solid and heavy carapace, but especially in the armature of the tail, which, in some cases at least, must have been a formidable weapon of defence. It is usual to call the glyptodonts "giant armadillos," but that term is more properly applied to certain huge animals, as large as a rhinoceros, which were true armadillos. The largest existing species of the group is hardly more than a yard long.

Among the hoofed animals, three of the native groups, the toxodonts, typotheres and litopterns, which were so remarkably abundant and varied in the Santa Cruz Miocene, persisted into the Pleistocene and then became extinct. Evidently they had begun to decline long before that epoch, possibly because of the competition of the more advanced and highly organized intruders from the north, though certain series continued to progress in size and differentiation of structure until the end of their career. One of the most characteristic of these animals was *Toxodon*, of which two skeletons are mounted in the La Plata Museum. The genus was found by Charles Darwin, who says of it: "Perhaps one of the strangest animals ever discovered; in size it equalled an elephant or megatherium, but the structure of its teeth, as Mr. Owen states, proves indisputably that it was intimately related to the Gnawers [*i. e., Rodentia*] . . . in many details it is allied to the Pachydermata: judging from

the position of its eyes, ears and nostrils, it was probably aquatic, like the Dugong and Manatee, to which it is also allied." Darwin's scanty materials led him to exaggerate the size of this extraordinary beast and his views as to its diverse relationships are not tenable from the modern point of view, but his brief description brings out the strangeness of structure in a vivid way. *Toxodon* ranged as far north as Nicaragua, but, so far as is known, did not enter North America proper.

Somewhat distantly related to *Toxodon* was the equally strange *Typotherium,* an animal of moderate size, which was the last of a very long series of native developments. Its permanently growing, chisel-like incisors are so similar to those of the rodents that the genus was long referred to that order. Typotheres were extremely numerous in the Santa Cruz times, but declined rapidly in relative importance after that and disappeared completely at the end of the Pleistocene.

Of all the many bizarre animals which swarmed in Pleistocene South America, none was more extraordinary than *Macrauchenia,* which, like *Toxodon,* was one of Darwin's discoveries, when he was on the memorable voyage of the *Beagle. Macrauchenia* was somewhat like a large camel in proportions, but of much heavier build. The head was relatively small and must have had quite a long proboscis, which added much to the grotesque appearance of the creature. The neck was very long, suggesting that the animal browsed upon trees, which is also indicated by the character of the teeth; the legs were long and heavy, the feet short and each provided with three toes. This was the last of the Litopterna, an exclusively South American group which had for a long period played a very conspicuous rôle in that continent, but, like the typotheres, had begun to decline in numbers after the Santa Cruz epoch.

The rodents of the South American Pleistocene do not offer much that is of particular interest. The presence of North American types of meadow-mice, which no longer exist in the southern continent, is a noteworthy fact, as is also the occurrence of *Megamys,* an extinct representative of one of the indigenous families. This was the largest of all known rodents, living or fossil, and rivalled the rhinoceros in size—for a rodent, a veritable monster.

From this comparison of the North and South American faunas, as they are revealed in the geological succession, certain facts stand out saliently. (1) It is evident that North America contributed much more extensively to the southern fauna than South America did to the northern. Even in the Pleistocene, when the movement of intermigration had reached its maximum and there were more mammalian types common to the two continents than at any other period, before or after, the number of Notogæan types found in North America was really very small; opossums, a few rodents, ground-sloths and glyptodonts complete the list. Of these only the opossums and the short-tailed porcupines have survived to modern times. On the other hand, the list of northern forms which, before or during the Pleistocene epoch, had invaded the southern continent, is very much longer; bears, cats, saber-toothed tigers, weasels, otters, skunks, raccoons, dogs of many kinds, rabbits, squirrels, rats, mice, horses, tapirs, peccaries, deer, antelopes, llamas and mastodons, all found their way into South America and most of them still inhabit that region. The short-faced bears, saber-toothed tigers and the mastodons became extinct everywhere; the horses died out completely in the western hemisphere, while the ante-

lopes and meadow-mice vanished from South America, though persisting in North America. The permanent contribution of South America to the northern fauna is, on the contrary, quite insignificant.

While it is impossible to say with any certainty just why the northern animals should have thus predominated over the southern, it is reasonable to conclude that it was due to the higher stage of intelligence and structural development which the former had attained. There can be no question as to this structural superiority, but such superiority, as we call it, does not always insure victory in the struggle for existence, victory largely depending upon the nature of the environment. It must be remembered that by no means all of the northern animals which invaded Notogæa were of North American origin; many were immigrants from the Old World, of different geological dates of arrival in the western hemisphere and correspondingly different degrees of modification. The repeated junction of North America with Asia made the former a part of Arctogæa, incomparably the greatest land area of the globe, and such immensity of connected lands is favorable to the higher evolution of terrestrial life. The comparative isolation of South America kept that continent in a relatively backward state.

(2) The very different degrees of likeness and unlikeness between the faunas of the two continents in the successive geological epochs point unmistakably to extensive geographical changes. Beginning with a time of radical difference, when the two faunas had almost nothing in common, the story goes on to tell of a period when an exchange of mammals began, gradually extending until a very considerable number of types common to both continents was found, and finally reducing the number of these common types to the present condition. The obvious interpretation of these facts is that the complete dissimilarity of animals was due to an equally complete separation of the continents and that a certain degree of likeness was brought about when a land connection was established. Well-founded as this conclusion appears to be, confirmation from a quite independent line of evidence would be welcome and such evidence is to be obtained from the geology of Central America and the Isthmus of Panama.

(3) Intermigrations between the Americas have always had to contend with serious obstacles and difficulties; otherwise, the interchanges of land animals would have been much more extensive than they ever became. Then, too, it would seem that there have been times in the past when migration was less difficult than it is at present, for now there is little or no indication of such movements. As was previously shown, the principal barrier to the spread of mammals over connected or continuous lands is climate, and it follows that the times of migration were those of more favorable climatic conditions. In the early Miocene, when the migrations probably began, the climate was much milder than at present, with less difference between the tropical and temperate regions. Through nearly the whole of the Tertiary period these conditions persisted, though with a slowly progressive refrigeration, and even in the Interglacial of the Pleistocene, the amelioration of climate was such that migration was rendered more practicable than it is under existing circumstances.

The geological structure and history of the lands around the Caribbean Sea are not nearly so well known as would be desirable, but certain very significant facts have already been ascertained. Especially is this true of the Isthmian Canal Zone,

which has been studied by Macdonald. There is very little direct information, as yet, regarding the condition of Central America and the Isthmus of Panama during the Eocene, whatever rocks there may be in the region of Eocene or earlier date being buried under newer formations. It is clear, however, that in the succeeding Oligocene epoch the whole Caribbean region was extensively submerged; the Greater Antilles were much reduced in size and nearly the whole of Central America was under water, a broad sea separating North and South America, though doubtless with scattered islands. On the Caribbean side of the Isthmus is a very thick mass (estimated at 2,500 feet) of Oligocene strata, the Gatun formation, which is crowded with marine fossils. The Culebra Hills, through which the great cut has been made, are chiefly built up of volcanic materials, lava streams, mud-flows, tuffs, etc., in a very complicated arrangement, and running through the cut may be traced thin bands of a marine limestone, which carry Oligocene fossils. The evidence of submergence is thus complete, but the date of upheaval can not be very definitely fixed. Except for a narrow strip of Pleistocene on the Caribbean coast, no marine rocks later than the Oligocene have been found on the Isthmus and it would be natural to conclude that the elevation came at the close of that epoch. Some allowance must, however, be made for erosion and it is quite possible that early Miocene rocks were formed and have since been swept away. The ground-sloth in the middle Miocene of Oregon is proof that the connection was established at least as early as that.

In the Pliocene and perhaps early Pleistocene the isthmian region was considerably broader than it is now and it is probable that the flat lands lying along the then existing coast afforded a comparatively easy highway of migration, the chief obstacles to which were climatic rather than topographical, but during some part of the Pleistocene the Isthmus was again depressed and narrowed even beyond its present limits, as is shown by the fringe of marine deposits along the Caribbean coast.

Central America, like the West Indies, belongs zoologically to South America and forms a part of the Neotropical Region. This fact is not altogether easy of explanation. It may be that the Isthmus connected South and Central America at a time when the latter was still separated from the northern continent. Were this the case, the southern fauna would have had the advantage of possession, when the northern invasion began. On the other hand, the cause may be entirely climatic and that this is the rightful conclusion is indicated by the distribution of animals now obtaining in Mexico. The high table-land of that country contains an extension of the North American fauna, while the tropical lowlands are South American.

It is a truism to say that the Isthmus of Panama is the strategic key to the zoological relations of North and South America, and yet it was not necessarily so, as other lines of communication might conceivably have been established. So far as our knowledge extends, however, the geographical events in the history of the Isthmus dominated the biological interrelations of the continents which it now unites. When the Isthmus was submerged, South America was in a state of nearly or quite complete isolation and developed a highly peculiar fauna, few elements of which were shared with any other continent, and which was as unique in its way, though on a higher plane, as is the Australian. It was, so to speak, a highly interesting experiment in evolution; a great continent,

with varied climate and a great diversity of conditions, mountains and valleys, forests and open plains, left through long ages entirely to its own resources, was the closed arena of rapid development divergent from the rest of the world. The result is plainly obvious now. Though the elevation of Central America and the Isthmus into land joined Notogæa with the northern continent and the way of migration thus opened led to an extensive infusion of northern elements in the southern fauna, South America still remains, after Australia, the most peculiar region of the earth.

North America had quite a different fate; its connection with the south was a mere episode which led to the transitory reception of a considerable number of Notogæan forms and the permanent establishment of a very few. Its oft-repeated connection with the Old World was far more significant from the zoological point of view, for that maintained the essential community of mammalian life all over the northern hemisphere. To this connection it is due that North America is a part of Arctogæa and that its Arctic and Boreal zones are inseparable from the great Holarctic Region of Europe and Asia. In the Pliocene and Pleistocene, North America was the meeting-ground of currents of migrating animals, from the west and from the south and for a time the fauna was of an exceptionally composite character, Old World and Notogæan elements mingling with the richly variegated indigenous stocks. But this condition was much modified by the Pleistocene extinctions which almost entirely exterminated the invaders from the south and greatly reduced the number of autochthonous forms. The destruction of immigrants from the Old World was less extensive and thus the zoological relations of North America in the Pliocene and Pleistocene were quite different from what they are now.

The problems which deal with the possible connections of South America with continents other than North America and especially with Africa and Australia, are extraordinarily interesting from many different points of view, but there is no time to enter upon a discussion of them here, nor are they altogether germane to the subject before us, which is the zoological relations of the western hemisphere as conditioned by the Isthmus of Panama and its geographical history.

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THE NEEDS OF APPLIED OPTICS[1]

We have formed this Association for the Advancement of Applied Optics because we believe that the interests of all branches of applied optics may be materially furthered by such an organization. It seems fitting, therefore, to devote this first meeting to a discussion of the needs of applied optics and to the outlining of plans for securing the advancement desired.

The interests of every one who uses light are affected by applied optics in its broader interpretation. In the formation of this society we have invited the cooperation of all who are directly interested in the study and use of light and of optical instruments of all kinds. We therefore include, among those whose interests we aim to serve, astronomers, designers of optical instruments, illuminating engineers, photographers, ophthalmologists, photometrists, colorists, petrologists, microscopists and all investigators of optical problems. The field to be covered is broad and the interests affected many and diverse.

[1] An address inaugurating the formation of the Association for the Advancement of Applied Optics delivered at the first meeting held in Rochester, January 4, 1916.